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Use of dihaploids in the breeding of *Solanum tuberosum* L.

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by

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2. — 1971. Use of dihaploids in the breeding of *Solanum tuberosum* L. I. Cytological considerations. — *Ibid.* 69: 83—100.
3. — 1972. Use of dihaploids in the breeding of *Solanum tuberosum* L. II. Crossability behavior. — *Ibid.* 70: 135—152.



Dedicated to:

John S. Niederhauser,
pioneer in potato-breeding in Mexico, and most
constant friend to all those, young and old,
engaged in potato research

and to:

Thore Denward,
without whose guidance, unfailing patience,
and most generous help this work could never
have seen the light of day.



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"By and large the development of resistant varieties must be looked upon as a continuing program. The potential variability of most pathogens (including viruses) will not permit any currently successful variety to remain so for an indefinite period" (WALKER 1959).

Introduction

The breeding of the common potato can be traced back to pre-conquest times when natives of Latin-America selected those plants which produced a higher yield or those which were better suited to their own special necessities. The introduction of the potato into Europe during the XVIth century was followed by a period lasting almost 350 years during which breeding was based on a very restricted range of genetic variability (ROSS 1966).

Progress in the taxonomy of the genus *Solanum* as well as in the knowledge of host-pathogen interaction between wild species of *Solanum* and several disease-causing organisms brought in their wake a wide-spread recognition that these wild species of *Solanum* constitute the natural reservoir from which resistance to diseases and pests as well as to adverse environmental conditions may be obtained.

Several methods have been tried to make use of the variability present in wild species of *Solanum* (HOWARD 1963). The obtaining of dihaploids from commercial varieties of *S. tuberosum* can be regarded as one of the most important achievements for both basic and applied studies in the potato (PELOQUIN, HOUGAS and GABERT 1966). The present investigation serves to emphasize, however, that several problems have to be solved before the successful use of dihaploids in the breeding of the common potato can be considered a reality. These problems are mainly related to self- and cross-incompatibility, heterozygosity and restoration of the tetraploid level.

Some general information about potato-breeding may be convenient before we embark upon the main subject of this thesis. Firstly, we have to recall that from the genetic point of view it is difficult to create a genotype which fits the requirements of human beings as well as the ecology in a particular habitat. This has given rise to the continuous use of very old

varieties which do not possess the necessary resistance to the main pathogens although they are well adapted to the growing and processing techniques. Usually this situation is more evident in countries with a high consumption per capita, where farmers and consumers are so used to one or two varieties that they will not accept a new one. In countries such as Mexico, where the dietetic value of the potato has not yet been sufficiently appraised, and where consumption per capita is very low (10 kilograms/year in contrast to 80 kilograms/year in Sweden), it would seem to be of little value to increase a production based on the use of varieties that involve considerable expenditure per hectare. These varieties have been considered of high quality but only yield a satisfactory harvest if they receive several chemical treatments against late blight. The processing industry in Mexico is so incipient that the production of these varieties has to be consumed as cooked potatoes. Varieties with a high yield and with a high resistance to late blight have not been well received by farmers on account of their supposed "lack of quality". However, studies on their dry matter content have succeeded in getting them accepted for direct consumption (CADENA-HINOJOSA 1967). For a variety of reasons, however, it would appear that farmers all over the world tend to choose as the best variety the potato which needs a large amount of mechanical and chemical treatment, no matter how much it may add to environmental pollution.

Mexico is regarded as one of the most suitable natural greenhouses in the world for the breeding of several crops, potato being no exception. Native diploid and hexaploid tuber-bearing species have been proved to be carriers of genes for resistance to insect pests, fungal and virus diseases. Moreover, some localities, especially the Toluca Valley, have been found

to be a bottle-neck for field resistance tests to late blight. It is necessary to accept the fact that the breeding of the potato in Mexico as well as in any other country has to be carried out to meet the actual needs of the consumers. This thought was uppermost in the mind of the former potato-breeders (NIEDERHAUSER pers. comm.), whose first aim was to produce varieties with a high yield and a high resistance to late blight. These potatoes should also be suitable as a subsistence crop produced by the Mexican farmers as a collateral activity. Another aim to be fulfilled was the incorporation of desirable genes from wild species into well-adapted but disease-susceptible local varieties (criollas) on account of their great selling possibilities and because they are still grown in more than 50 % of the total national area. Many advanced lines and many new varieties endowed with several positive agronomical characters have been created by means of classical breeding methods, but unfortunately, their total part in the national product is lower than 5 %.

Owing to the small amount of potatoes used by the processing industry in Mexico, it is desirable to stress the importance not only of an increase in the cultivation of those varieties which respond better to the attack of late blight and other main diseases but also to give careful consideration to the types of potato most popular among Mexican consumers. On the other hand, attention should be paid to the creation of varieties which combine the requirements of direct consumption with those of the future potato food industry.

Breeding by means of dihaploids

There are many features which make *S. tuberosum* dihaploids a very suitable material for a breeding program. (1) The minimal-size population to include a desirable genotype is lower at the diploid than at the tetraploid level. (2) There are about 70 wild and cultivated diploid species which are carriers of desirable genes (ROWE 1969). (3) It is possible that

breeding at the diploid level will reveal some valuable characters which have passed unnoticed at the tetraploid level.

The following is a brief description of the results obtained when using dihaploids in the breeding of the common potato, from their cytological identification until the creation of advanced tetraploid clones (SOSA and HERNÁNDEZ DE SOSA 1970, 1971 and 1972).

A. Field resistance to *Phytophthora infestans* (MONT.) DE BY. and general variability

Dihaploids derived from varieties with a high field resistance showed a higher average degree of resistance than dihaploids derived from susceptible varieties. The obtaining of dihaploids, some with a much lower and other with a much higher degree of resistance than that of the tetraploid mother, indicates that late-blight resistance seems to be controlled by several factors whose segregation by the tetraploid mother permits the production of dihaploids showing continuity from susceptibility to resistance. High resistance was almost always correlated to a bad tuber shape. It was possible, however, to obtain dihaploids with a good tuber shape and with an acceptable resistance.

Flower colours in dihaploid clones were almost the same as in the tetraploid mothers. Some dihaploids showed different abnormalities regarding flower structure. In some clones the number of anthers was higher than 5, and in others there was a tendency to form double flowers (HERNÁNDEZ DE SOSA 1967). The inheritance of these abnormalities has been discussed by KOOPMANS (1951) and GRUND (1970 a, b). Some clones with 6 to 8 anthers produced a great quantity of pollen. On the other hand, some dihaploids with a normal floral structure did not produce any pollen at all. This indicates that flower morphogenesis, anther development and microsporogenesis are processes which are controlled by different factors.

Plant height, as any other quantitative character, was represented by a complete gamut of sizes. In addition, genetic dwarfs were not uncommon (HERNÁNDEZ DE SOSA l.c.). Very few

clones produced the same or higher tuber number than the mother and tubers from dihaploids were also smaller. Generally speaking, it can be said that dihaploids resemble their mother in many characters. The degree of this resemblance is probably correlated to the degree of homozygosity of the tetraploid mother.

B. Genomic relationships

Chromosome behavior during meiosis was different among dihaploids extracted from different tetraploid varieties as well as among dihaploids extracted from the same variety. The fact that chromosome pairing is achieved almost completely between two 12-chromosome sets seems to indicate that meiotic abnormalities are mainly due to factors controlling different phases during meiosis rather than to differences in the chromosomal structure of the genomes.

Almost the same meiotic abnormalities (univalents, multivalents, bridges, etc.) were also found in hybrids derived from crosses between dihaploids or hybrid dihaploids and some diploid species. An analysis of variance of chiasma frequency, carried out in these hybrids, revealed that chromosomes of dihaploids from tetraploid Atzimba, or chromosomes of hybrids derived from crosses between Atzimba dihaploids and diploid clones from groups Phureja and Andigena, form chiasmata at almost the same frequency with chromosomes from different diploid species belonging to three different taxonomic series. These results, together with those obtained from studies of other meiotic phases, seem to indicate that in this material chromosome differentiation has been too weak to affect chromosome pairing significantly, irrespective of the fact that chromosomes from dihaploids, have been settled for a long time at the tetraploid level.

Studies on chromosome behavior in dihaploids of *S. tuberosum* make it difficult to omit considerations regarding the basic chromosome number in the genus *Solanum* as well as considerations regarding the putative diploid ancestor(s). The occurrence of multivalents in dihaploids as well as in hybrid dihaploids seems

to be caused by heterozygous translocations rather than by homology within sets of four chromosomes. Studies of diakinesis have revealed the presence of a large bivalent in both primary dihaploids and hybrid dihaploids, which hardly can be mistaken for any other.

Another source of evidence in favor of a 12-chromosome basic number comes from population studies concerning albinism. Preliminary results strongly suggest that segregation of this character is based on a disomic inheritance system (SOSA and HERNÁNDEZ DE SOSA, unpublished data).

The almost equal chiasma frequency between chromosomes of Atzimba hybrid dihaploids and chromosomes of diploid species, suggests that several diploid species could have been involved in the formation of what is known as the common potato. The production of unreduced gametes in all studied dihaploids and hybrid dihaploids favors the idea that our tetraploid cultivar could have been derived several times from different diploid populations in different localities.

C. Crossability behavior

One of the first aims in the breeding of the common potato by means of dihaploids is the exploitation of the wide variation found in wild diploid and hexaploid species. Crosses between dihaploids belonging to different taxonomic groups of the cultivated potato, as well as crosses between dihaploids belonging to the same taxonomic group were liable to produce seed. However, crosses between dihaploids extracted from the same tetraploid variety did not produce seed. Some dihaploid clones were shown to be self-compatible. Seeds/fruit ratios in hybrids between dihaploids (or hybrid dihaploids) and some diploid species were quite acceptable. Self- and cross-incompatibility were considered to have played a great part in seed production. It was not possible, however, to characterize the incompatibility system operating in the material studied. Whatever its genetic background it was certainly affected by other genetic factors and by environmental factors as well. On the other hand, other types

of incompatibility, e.g., one-way incompatibility, were found to play a great part in the success or failure of the crosses. Here again the crossing behavior found in our material did not follow the typical pattern of a one-way incompatibility system. Nevertheless, whatever the inheritance of pollen grain behavior and whatever the genetics of seed production, it was possible to obtain recombinants, some of which with good agronomical characters, from certain crosses between dihaploids as well as from dihaploids or hybrid dihaploids crossed with diploid species.

Crosses between colchicine-induced tetraploids did not increase seed set. However, crosses between colchicine-induced tetraploids from selected dihaploids or hybrid dihaploids and commercial varieties, permitted the transfer of desirable characters, e.g., resistance to late blight, from the diploid to the tetraploid level.

It should be pointed out that in the present material crosses between dihaploids and tetraploid varieties did not result in tetraploid offspring as was the case in other material (HAN-NEMAN and PELOQUIN 1967).

D. Colchicine-induced tetraploids and dihaploids vs. their tetraploid counterpart*

The doubling of the chromosome complement of some tuber-bearing species of *Solanum* by means of colchicine has played an important part in the breeding of the common potato. Several diploid wild species have been doubled and crossed to tetraploid cultivars (MAGOON, COOPER and HOUHAS 1958).

The colchicine treatment of the material studied was carried out according to the technique of ROSS, DIONNE and HOUHAS (1967). Complete tetraploid plants were not easily obtained but chimerical plants, where the chromosome number of the pollen mother cells was found to be doubled, were willingly accepted for breeding purposes.

Different chromosome numbers were found in tissues assumed to have been derived from

the three germinal layers. Plants with the following chromosome numbers were not uncommon: $L_I = 4x$, $L_{II} = 2x$, $L_{III} = 4x$; and $L_I = 4x$, $L_{II} = 4x$, $L_{III} = 2x$. Some of these plants showed the same chimerical composition after two vegetative generations.

As pointed out before, breeding at the diploid level may lead to a disclosure of new potentialities in diploid potatoes. An analysis of variance in eight diploid populations derived from crosses between dihaploids and hybrid dihaploids showed that samples from the same family displayed a greater variation for several characters, e.g., tuber-yield, when grown in the field than when grown in the greenhouse. A multiple regression analysis in those populations gave the impression that some independent variables accounted in a higher or lower degree for the variation of the dependent variable (tuber-yield) depending upon whether samples from the same family were grown in the greenhouse or in the field.

The low tuber-yield of raw colchicine-induced tetraploids found in our material is in accordance with the idea of a disturbed genetic balance due to the change from $2x$ to $4x$. This disturbed genetic balance has been observed in doubled hybrid dihaploids (ROWE 1967), in some other cultivars (HAGBERG and ÅKERBERG 1962) and in natural populations (STEBBINS 1971). However, crosses between such colchicine-induced tetraploids and commercial varieties led to the production of clones with a high agronomical potentiality.

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